Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

ON THE OSMOTIC PRESSURE OF THE TISSUE FLUIDS OF JAMAICAN LORANTHACEAE PARASITIC ON VARIOUS HOSTS[1]

J. Arthur Harris and John V. Lawrence

I. Introductory Remarks

This paper, which is one of a series on various physiological, ecological, phytogeographic, and evolutionary problems involving a knowledge of the physico-chemical properties of vegetable saps, has for its object the presentation of a series of observational data on one phase of the water-relations of tropical Loranthaceae—the osmotic pressure of their tissue fluids in comparison with that of their hosts.

Since our method of attack upon the physiology of the Loranthaceae is so far as we are aware quite novel, it has seemed most expedient to focus attention sharply and practically exclusively upon the actual results of our studies, reserving a detailed discussion of the literature until other work now planned and under way has been completed.

Whatever the answer to the mooted question of the nature of the solutes obtained by the parasite from its host—whether solely mineral or both mineral and plastic—the nature and the magnitude of the forces by which the solution containing these substances is drawn from the tissues of the host is a subject of fundamental importance.

Furthermore, few botanists would, we believe, be inclined to question the validity of the proposition that among these forces one of the fundamental variables is the osmotic pressure of the fluids contained in the tissues of the two organisms.[2]

---

[1] Results of investigations carried on at Cinchona, by courtesy of the British Association for the Advancement of Science and the Jamaican Local Government, under the joint auspices of the Department of Botanical Research and the Department of Experimental Evolution of the Carnegie Institution of Washington, and with the collaboration of the New York Botanical Garden.

[2] As far as we are aware the only botanists who have actually published this view are MacDougal and Cannon (1910) and MacDougal (1911*a*, 1911*b*), who considered a higher osmotic pressure in the sap of the engrafted organism to be one of the essentials of experimentally induced parasitism.

We have therefore determined by means of the cryoscopic method the osmotic pressure of the tissue fluids of host and parasite.

II. Materials and Methods

In the late winter and early spring months of 1915, we had the opportunity of spending some weeks in a study of the concentration of the saps of the plants of the Coastal Deserts and of the Montane Rain Forest of the Blue Mountains of Jamaica, splendidly described and illustrated by Shreve (1914). In the latter habitat Loranthaceae are abundant. York (1913) has given a detailed account of the morphology of two of the seven species which we have studied.

The parasites, structurally and physiologically considered, fall into two groups, those with and those without leaves.

The leaves of Phthirusa and Phorodendron may be looked upon as comparable with those of the host. Such can not legitimately be assumed of the green stems of the three (physiologically) leafless Dendrophthora species. In all the determinations based on these species, we had some difficulty in deciding what parts of the tissue of the parasite to include. It would obviously be quite illegitimate to compare the most tender recent growth of the parasite with the matured leaves of the host. It would also be quite wrong to draw the comparison between juices pressed from the oldest stems of the parasite with the leaves of the host tree. Possibly the best method would have been to scrape the green tissue from the outside of the parasite stems, but this would have entailed a very great deal of time and would have exposed the constants to obvious criticisms. Furthermore this method while applicable to *Dendrophthora gracilis* and *D. opuntioides* could not well be used for *D. cupressoides*. We decided, therefore, to include the whole of the obviously mature axis tissue, omitting only the very young growth, when such was present, and the older heavier stems which while once physiologically leaf homologs could not possibly be still so considered.

The technique used was very simple. Samples of the tissue of the parasite and host were collected in test tubes of about 100 cc. capacity and taken to the laboratory for freezing by immersion for several hours in an ice and salt mixture. The sap was then extracted by pressure in a small heavily tinned press bowl with a powerful hand screw. After filtering, the freezing point lowering of the sap was determined by the use of a thermometer graduated in hundreths of degrees with divisions sufficiently large to allow of reading to approximately thousandths of degrees. Ether or carbon bisulphide vaporized by a dried air current in a Dewar bulb was used in determining the freezing point of the sap.

In many instances a cloudiness or flocculent precipitate similar to that described by Gorke (1906) was observed when the sap approached the freezing point or passed it in undercooling. We had no facilities for any investigation of these substances but believe their presence does not greatly, if at all, influence our results.

The results are recorded in degrees depression, Δ, corrected for undercooling, and in atmospheres pressure, P, from a table published elsewhere (Harris and Gortner, 1914).

III. Presentation and Analysis of Data

We were able to make freezing point determinations on seven species representing three genera of Loranthaceae, parasitic upon a considerable number of hosts. Altogether 44 samples of parasitic tissue were used. In 42 cases sap was also extracted from the leaves of the host. .

The results, arranged primarily by the species of parasites and secondarily by the magnitude of the freezing point lowering, appear in the following protocol. For convenience of reference our field numbers have been retained. The values of Δ and P found for the parasite are given at the extreme right, opposite the host on which it was taken. Those found for the tissues of the host are placed immediately below the name of the host species. The + and − values given below the constants for the parasite show whether they are larger or smaller than those obtained from the tissue of the host, and the magnitude of the difference.

I. Phoradendron flavens (Sw.) Griseb.

538. On *Guarea Swartzii* DC. . $\Delta = 1.27$, $P = 15.3$
March 18. $\Delta = 0.90$, $P = 10.8$ $+0.37$, $+4.5$
528. On *Guarea Swartzii* DC. $\Delta = 1.34$, $P = 16.2$
March 18. $\Delta = 1.02$, $P = 12.3$ $+0.32$, $+3.9$

II. Phthirusa lepidobotrys (Griseb.) Eichl.

104. On *Dodonaea jamaicensis* DC. $\Delta = 1.24$, $P = 14.9$
Feb. 7. $\Delta = 1.09$, $P = 13.1$ $+0.15$, $+1.8$
510. On *Viburnum villosum* Sw. $\Delta = 1.36$, $P = 16.4$
March 18. $\Delta = 1.15$, $P = 13.9$ $+0.21$, $+2.5$

292. On *Duranta repens* L.	$\Delta = 1.39$, $P = 16.7$
Feb. 28. $\Delta = 1.29$, $P = 15.5$	$+ 0.10$, $+ 1.2$
280. On *Hedyosmum nutans* Sw.	$\Delta = 1.42$, $P = 17.1$
Feb. 26. $\Delta = 0.73$, $P = 8.8$	$+ 0.69$, $+ 8.3$
109. On *Baccharis scoparia* (L.) Sw. Old leaves,	$\Delta = 1.45$, $P = 17.4$
Feb. 7, Host not taken. New leaves,	$\Delta = 1.16$, $P = 13.9$
265. On *Dodonaea jamaicensis* DC.	$\Delta = 1.59$, $P = 19.1$
Feb. 26. $\Delta = 1.41$, $P = 16.9$	$+ 0.18$, $+ 2.2$

III. PHTHIRUSA PARVIFOLIA (Sw.) Eichl.

133. On *Clethra occidentalis* (L.) Steud.	$\Delta = 1.15$, $P = 13.8$
Feb. 9. $\Delta = 0.77$, $P = 9.3$	$+ 0.38$, $+ 4.5$
356. On *Mecranium purpurascens* (Sw.) Triana	$\Delta = 1.16$, $P = 13.9$
March 4. $\Delta = 0.77$, $P = 9.2$	$+ 0.39$, $+ 4.7$
203. On *Vaccinium meridionale* Sw.	$\Delta = 1.18$, $P = 14.2$
Feb. 18.[3] $\Delta = 1.25$, $P = 15.1$	$- .07$, $- 0.9$
481. On *Palicourea alpina* (Sw.) DC.	$\Delta = 1.23$, $P = 14.8$
Feb. 16. $\Delta = 0.83$, $P = 10.0$	$+ 0.40$, $+ 4.8$
483. On *Clethra occidentalis* (L.) Steud.	$\Delta = 1.28$, $P = 15.4$
Feb. 16. $\Delta = 0.68$, $P = 8.2$	$+ 0.60$, $+ 7.2$
537. On *Quercus* sp.	$\Delta = 1.30$, $P = 15.6$
March 19. $\Delta = 1.10$, $P = 13.3$	$+ 0.20$, $+ 2.5$
364. On *Ilex montana* (Sw.) Griseb.	$\Delta = 1.31$, $P = 15.8$
Sap from host was insufficient for a determination.	
246. On *Vaccinium meridionale* Sw.	$\Delta = 1.38$, $P = 16.7$
Feb. 24. $\Delta = 1.34$, $P = 16.1$	$+ 0.04$, $+ 0.6$
484. On *Vaccinium meridionale* Sw.	$\Delta = 1.39$, $P = 16.7$
March 16.[4] $\Delta = 1.32$, $P = 15.9$	$+ 0.07$, $+ 0.8$
292. On *Duranta repens* L.	$\Delta = 1.40$, $P = 16.8$
Feb. 28. $\Delta = 1.29$, $P = 15.5$	$+ 0.11$, $+ 1.3$
204. On *Baccharis scoparia* (L.) Sw.	$\Delta = 1.42$, $P = 17.1$
Feb. 18. $\Delta = 1.15$, $P = 13.8$	$+ 0.27$, $+ 3.3$
196. On *Dendrophthora gracilis* (Griseb.) Eichl.	$\Delta = 1.49$, $P = 17.9$
Feb. 17. $\Delta = 1.26$, $P = 15.2$	$+ 0.23$, $+ 2.7$
247. On *Baccharis scoparia* (L.) Sw.	$\Delta = 1.50$, $P = 18.0$
Feb. 27. $\Delta = 1.27$, $P = 15.4$	$+ 0.23$, $+ 2.6$
265. On *Dodonaea jamaicensis* DC.	$\Delta = 1.63$, $P = 19.6$
Feb. 26. $\Delta = 1.41$, $P = 16.9$	$+ 0.22$, $+ 1.7$

IV. PHTHIRUSA PAUCIFLORA (Sw.) Eichl.

110. On *Baccharis scoparia* (L.) Sw.[5] Old leaves	$\Delta = 1.41$, $P = 17.0$
New leaves	$\Delta = 1.31$, $P = 15.7$
No determination made for the host.	

---

[3] New leaves of the host gave: $\Delta = 0.93$, $P = 11.2$.

[4] New leaves of the host gave: $\Delta = 1.18$, $P = 14.2$.

[5] The identity of the parasite is in this case not quite certain.

508. On *Citharexylum caudatum* L.	$\Delta = 1.59$,	$P = 19.2$
March 18. $\Delta = 2.03$, $P = 24.4$	-0.44,	-5.2
265. On *Dodonaea jamaicensis* DC.	$\Delta = 1.71$,	$P = 20.5$
Feb. 26. $\Delta = 1.41$, $P = 16.9$	$+0.30$,	$+3.6$

V. DENDROPHTHORA CUPRESSOIDES (Macf.) Eichl.

130. On *Miconia quadrangularis* (Sw.) Naud.	$\Delta = 0.99$,	$P = 11.9$
Feb. 9. $\Delta = 0.87$, $P = 10.5$	$+0.12$,	$+1.4$
226. On *Miconia quadrangularis* (Sw.) Naud.	$\Delta = 1.04$,	$P = 12.5$
Feb. 20. $\Delta = 0.94$, $P = 11.3$	$+0.10$,	$+1.2$
491. On *Miconia quadrangularis* (Sw.) Naud.	$\Delta = 1.08$,	$P = 13.0$
March 16. $\Delta = 1.07$, $P = 12.9$	$+0.01$,	$+0.1$
482. On *Miconia quadrangularis* (Sw.) Naud.	$\Delta = 1.16$,	$P = 14.0$
March 16. $\Delta = 0.98$, $P = 11.8$	$+0.18$,	$+2.2$
403. On *Miconia quadrangularis* (Sw.) Naud.	$\Delta = 1.17$,	$P = 14.1$
March 9. $\Delta = 1.11$, $P = 13.4$	$+0.06$,	$+0.7$
204. On *Baccharis scoparia* (L.) Sw.	$\Delta = 1.19$,	$P = 14.4$
Feb. 18. $\Delta = 1.15$, $P = 13.8$	$+0.04$,	$+0.6$
122. On *Rapanea ferruginea* (R. & P.) Mez	$\Delta = 1.25$,	$P = 15.1$
Feb. 9.[6] $\Delta = 0.96$, $P = 11.6$	$+0.29$,	$+3.5$
247. On *Baccharis scoparia* (L.) Sw.	$\Delta = 1.26$,	$P = 15.1$
Feb. 24. $\Delta = 1.28$, $P = 15.4$	$+.02$,	$+0.3$
486. On *Rapanea ferruginea* (R. & P.) Mez	$\Delta = 1.45$,	$P = 17.4$
March 16. $\Delta = 1.07$, $P = 12.9$	$+0.38$,	$+4.5$

VI. DENDROPHTHORA GRACILIS (Griseb.) Eichl.

123. On *Eugenia virgultosa* (Sw.) DC?	$\Delta = 0.91$,	$P = 10.9$
Feb. 9. $\Delta = 0.72$, $P = 8.7$	$+0.19$,	$+2.2$
180. On *Eroteum theoides* Sw.	$\Delta = 1.10$,	$P = 13.2$
Feb. 14.[7] $\Delta = 1.03$, $P = 12.4$	$+0.07$,	$+0.8$
481. On *Palicourea alpina* (Sw.) DC.	$\Delta = 1.12$,	$P = 13.5$
March 13. $\Delta = 0.83$, $P = 10.0$	$+0.29$,	$+3.5$
447. On *Vaccinium meridionale* Sw.	$\Delta = 1.19$,	$P = 14.3$
March 13. $\Delta = 1.36$, $P = 16.3$	$-.17$,	-2.0
374. On *Eroteum theoides* Sw.	$\Delta = 1.24$,	$P = 14.9$
March 6. $\Delta = 1.20$, $P = 14.5$	$+0.04$,	$+0.4$
284. On *Eroteum theoides* Sw.	$\Delta = 1.25$,	$P = 15.1$
Feb. 28. $\Delta = 1.15$, $P = 13.9$	$+0.10$,	$+1.2$
196. On *Cyrilla racemiflora* L.	$\Delta = 1.26$,	$P = 15.2$
Feb. 17. $\Delta = 1.18$, $P = 14.2$	$+0.08$,	$+1.0$
484. On *Vaccinium meridionale* Sw.	$\Delta = 1.34$,	$P = 16.1$
March 16.[8] $\Delta = 1.32$, $P = 15.9$	$+0.02$,	$+0.2$

[6] Young leaves of the host gave: $\Delta = 0.89$, $P = 10.7$.

[7] For new leaves: $\Delta = 1.30$, $P = 15.6$.

[8] For new leaves of host: $\Delta = 1.18$, $P = 14.2$.

VII. DENDROPHTHORA OPUNTIOIDES (L.) Eichl.

512. On *Dendropanax arboreum* (L.) Dec. & Pl. $\Delta = 1.13$, $P = 13.6$
March 18. $\Delta = 1.10$, $P = 13.3$ $+0.03$, $+0.3$
153. *Dendropanax arborum* (L.) Dec. & Pl. $\Delta = 1.16$, $P = 14.0$
Feb. 11. $\Delta = 1.11$, $P = 13.3$ $+0.05$, $+0.7$
509. On *Oreopanax capitatum* (Jacq.) Dec. & Pl. $\Delta = 1.17$, $P = 14.0$
March 18.[9] $\Delta = 1.53$, $P = 18.3$ -0.36, -9.8

As a basis of comparison for the individual determinations for the hosts, the average freezing point lowering and osmotic pressure based on all the determinations made, not merely those from plants on which parasites were found, are given in the accompanying table.

MEAN OSMOTIC PRESSURE IN SAP OF HOSTS

Species	Determinations	Mean Δ	Mean P
Baccharis scoparia	3	1.177	14.17
Citharexylum caudatum	4	1.950	23.43
Clethra occidentalis	2	0.725	8.75
Cyrilla racemiflora	1	1.180	14.20
Dendropanax arboreum	2	1.105	13.30
Dodonaea jamaicensis	3	1.183	14.23
Duranta repens	5	1.288	15.50
Eroteum theoides	4	1.143	13.78
Eugenia virgultosa	1	0.720	8.70
Guarea Swartzii	7	0.894	10.77
Hedyosmum nutans	1	0.730	8.80
Miconia quadrangularis	8	0.988	11.90
Mecranium purpurascens	2	0.770	9.25
Oreopanax capitatum	3	1.593	19.10
Palicourea alpina	6	0.675	8.12
Quercus	1	1.100	13.30
Rapanea ferruginea	4	1.078	12.98
Vaccinium meridionale	6	1.292	15.55
Viburnum villosum	1	1.150	13.90

A cursory glance over the differences shows at once that in the great majority of the cases the freezing point lowering of the parasite is distinctly greater than that of the host.

This result may be most emphatically brought out by a graphical representation of the constants in diagrams 1 and 2. In diagram 1 the amount of depression below the freezing point of pure water for both parasite (solid dots) and host (circles) is shown on the scale to the left. Here the determinations are arranged in order according to the freezing point lowering of the parasite. Diagram 2 is quite comparable except that in it the data are arranged according to the freezing point lowering of the juices of the leaves of the host plant.

---

[9] The young leaves of the host gave: $\Delta = 1.14$, $P = 13.8$.

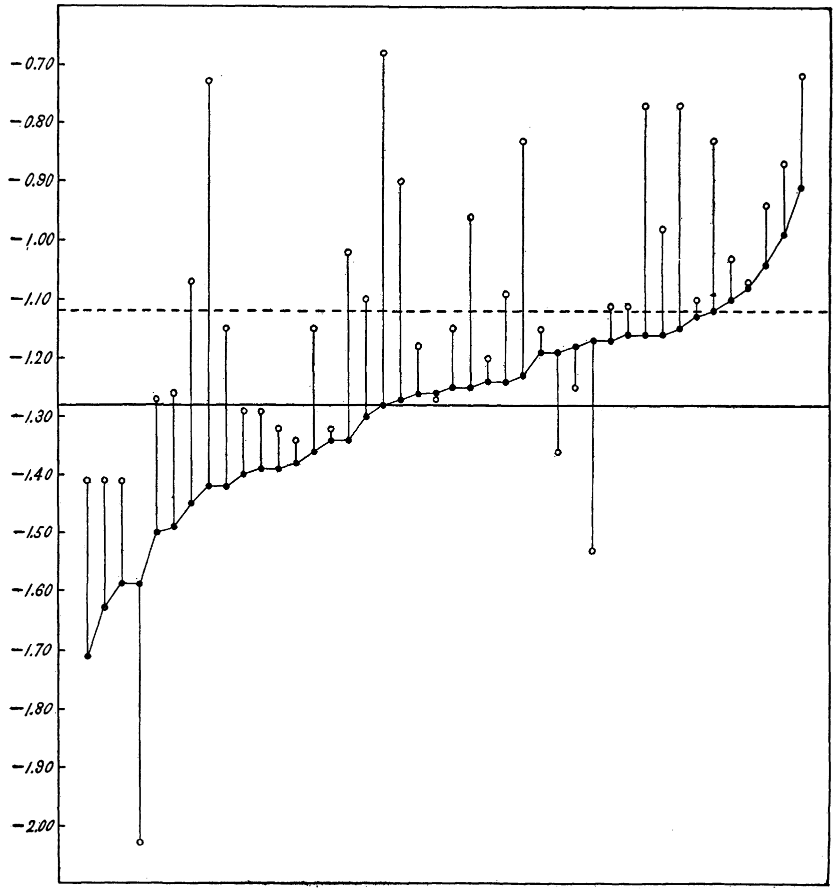

Diagram i. Freezing point of extracted sap of parasite (solid dots) and of host (circles). The determinations are arranged in order of magnitude of the values obtained from the parasite. The length of the lines connecting the dots and circles indicate on the scale to the left the amount of the difference between the freezing point of the sap of the two organisms. The mean value for the parasites is shown by the solid bar, that for the hosts by the broken line.

The differences between parasite and host are indicated by the lengths of the bars connecting the circles and solid dots.

With but five exceptions, of which one is trivial in magnitude, the parasites show distinctly greater freezing point lowering than their hosts. In other words, their tissue fluids are characterized by higher osmotic pressure.

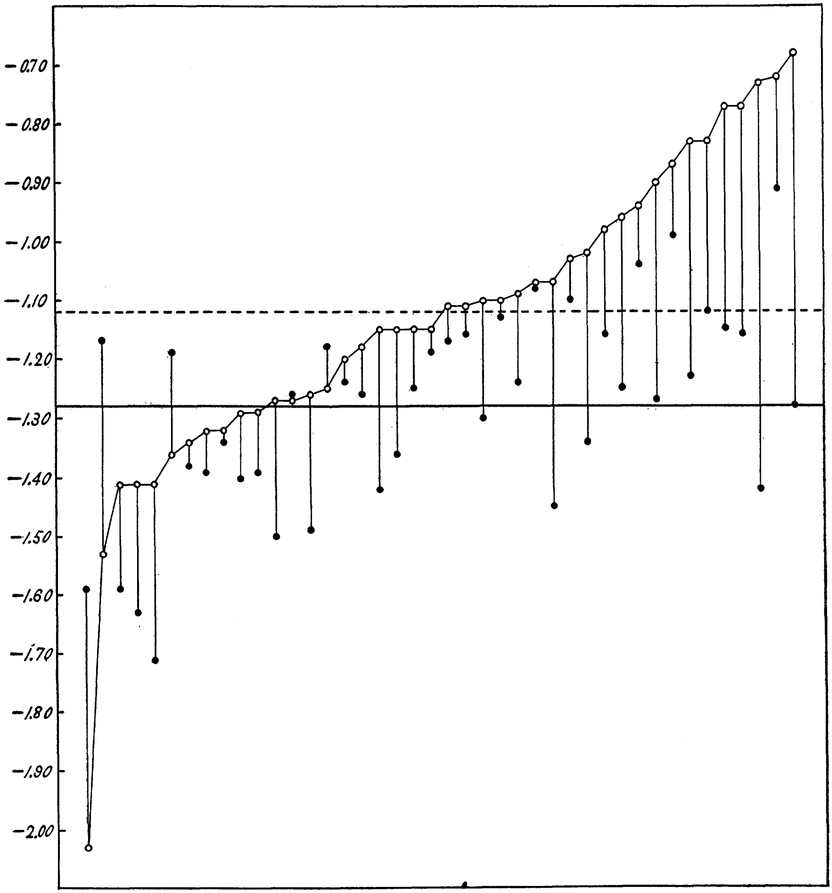

DIAGRAM 2. Determinations of freezing point of extracted sap of Loranthaceae and hosts, arranged in order according to the values for the latter. Compare explanation of Diagram 1.

Having recourse to averages for more exact comparison of the seven species of parasites with their hosts[10] we find:[11]

---

[10] The means are based upon the parasites which are accompanied by host determinations only, not upon all the freezings for the sap of the loranths. Thus the means for host and parasite are quite comparable.

[11] The bars indicate that the values of Δ and P are averages.

Phoradendron flavens, 2 determinations

For parasite . . . . $\bar{\Delta} = 1.305$, $\bar{P} = 15.75$
For host . . . . $\bar{\Delta} = 0.960$, $\bar{P} = 11.55$
Difference . . . . $+0.345$ $+4.20$

Phthirusa lepidobotrys, 5 determinations

For parasite . . . . $\bar{\Delta} = 1.400$, $\bar{P} = 16.84$
For host . . . . $\bar{\Delta} = 1.134$, $\bar{P} = 13.64$
Difference . . . . $+0.266$ $+3.20$

Phthirusa parvifolia, 13 determinations

For parasite . . . . $\bar{\Delta} = 1.347$, $\bar{P} = 16.19$
For host . . . . $\bar{\Delta} = 1.110$, $\bar{P} = 13.38$
Difference . . . . $+0.237$ $+2.81$

Phthirusa pauciflora, 2 determinations

For parasite . . . . $\bar{\Delta} = 1.650$, $\bar{P} = 19.85$
For host . . . . $\bar{\Delta} = 1.720$, $\bar{P} = 20.65$
Difference . . . . -0.070 -0.80

Dendrophthora cupressoides, 9 determinations

For parasite . . . . $\bar{\Delta} = 1.177$, $\bar{P} = 14.16$
For host . . . . $\bar{\Delta} = 1.048$, $\bar{P} = 12.62$
Difference . . . . $+0.129$ $+1.54$

Dendrophthora gracilis, 8 determinations

For parasite . . . . $\bar{\Delta} = 1.176$, $\bar{P} = 14.15$
For host . . . . $\bar{\Delta} = 1.098$, $\bar{P} = 13.24$
Difference . . . . $+0.078$ $+0.91$

Dendrophthora opuntioides, 3 determinations.

For parasite . . . . $\bar{\Delta} = 1.153$, $\bar{P} = 13.86$
For host . . . . $\bar{\Delta} = 1.246$, $\bar{P} = 14.96$
Difference . . . . -0.093 -1.10

The first point to be brought out by these averages is that the osmotic pressure of the tissue fluids of the leafless species is distinctly lower than that of the juices extracted from the leaf-bearing forms. The mean depressions in the former are 1.153°, 1.176° and 1.177°, as compared with 1.305°, 1.347°, 1.400°, and 1.650° in the latter.

The second is the emphasis laid upon the higher osmotic pressure of the fluids of the parasite as compared with those of the host.

In five of the seven comparisons the mean osmotic pressure of the juices of the parasite is higher than that of the leaf tissue of its hosts. The two exceptions are represented by only 2 and 3 determinations each. They cannot therefore be considered important, but are included for the sake of completeness merely. It is interesting to note that numerically they are smaller than the positive differences.

With numbers so small as those involved in the series of determinations for the individual species, it is idle to calculate probable errors. This has, however, been done for the whole series.[12]

The results are:

For parasites $\bar{\Delta} = 1.282 \pm .018$, $\bar{P} = 14.43$
For hosts $\bar{\Delta} = 1.129 \pm .026$, $\bar{P} = 13.59$
$+ 0.153 \pm .032$ $+ 1.84$

The difference is over four and one half times as large as its probable error.

In the diagrams and the averages we have included every pair of determinations available for the Jamaican series to avoid any possible criticism concerning the selection of data. Some of the cases in which the leaves of the host are recorded as exhibiting a higher osmotic pressure than those of the parasite are perhaps capable of explanation. Consider these cases in detail.

The exceptions to the rule of the higher osmotic pressure of the sap of the parasite are the following:

203. *Phthirusa parvifolia* $\Delta = 1.181$
on *Vaccinium meridionale* $\Delta = 1.252$
0.071

247. *Dendrophthora cupressoides* $\Delta = 1.258$
on *Baccharis scoparia* $\Delta = 1.276$
0.018

447. *Dendrophthora gracilis* $\Delta = 1.19$
on *Vaccinium meridionale* $\Delta = 1.355$
0.164

508. *Phthirusa pauciflora* $\Delta = 1.593$
on *Citharexylum caudatum* $\Delta = 2.027$
0.434

509. *Dendrophthora opuntioides* $\Delta = 1.165$
on *Oreopanax capitatum* $\Delta = 1.525$
0.360

---

[12] Statistically the process of combination of diverse species of parasites and of the various species of hosts seems quite legitimate, since the heterogeneity will tend to *increase* the magnitude of the calculated probable error.

In considering these exceptions it is important to note that the differences between parasite and host observed in this series as a whole are not large. The average differences for 42 determinations, regarding signs, is 0.154° while for the 37 cases in which the osmotic pressure of the parasite is greater than that of the host the average difference is only 0.203°.

Working as we did under many difficulties the greatest exactness in the constants cannot be expected. In at least one of these exceptions the difference between the freezing point lowering of the two organisms is so small that it may be due to purely experimental errors. Thus one would hardly assert that such a difference as 0.018° for Dendrophthora on Baccharis furnishes any valid proof that the osmotic pressure of the sap of these parasites is really lower than that of the leaves of their hosts.

With regards to these exceptions the following biological factors should be pointed out.

In the case of Collection 203, the value for the parasite is among the three smallest out of the 14 made for *Phthirusa parvifolia*. It may, therefore, be actually too small. The host tree had apparently been injured by fire recently. Old and young leaves of the host were taken. The young leaves gave only $\Delta = 0.931$. Thus the parasite ($\Delta = 1.181$) shows a concentration distinctly higher than do the young leaves of the host which are drawing their water in competition with the old ones.

The difference between the freezing point of *D. cupressoides* and its host, *B. scoparia*, is, as has already been pointed out, so slight that it might easily be due to an error in the determination of the freezing points alone. The constant for Baccharis is the highest secured for that species, which because of the hardness of its tissues presents some difficulty in the extraction of sap. Another point will be mentioned below.

Thus of the 42 comparisons there seem to be only three, that is those numbered 447, 508 and 509 in which the evidence of a superior osmotic pressure of the leaves of the host can be given any weight at all. These three cases are particularly interesting.

Note first of all that two of these three exceptions are leafless and rather thick stemmed shrubs, *Dendrophthora gracilis* and *D. opuntioides*. It is quite possible, as explained above, that in these cases there has been included a considerable amount of juice from woody tissue not at all comparable with the leaves of the host.[13]

Note too that while the juices of *D. opuntioides* gave a freezing point lowering of 0.360° less than that of the old leaves of Oreopanax, they gave a depression slightly greater than that of young Oreopanax leaves from the same tree, *i. e.*, $\Delta = 1.165$ as compared with $\Delta = 1.144$. The older leaves of Oreopanax gave a juice which was too gelatinous to filter. Whether or not this has influenced the accuracy of the determination of the freezing point of the host leaves we cannot assert.

There remains but one further exception, *Phthirusa paucifolia* on *Citharexylum caudatum*. At first sight the Δ of the host seems suspiciously high, but the three other determinations for this species made on trees from which parasites were not secured give $\Delta = 1.772$, $\Delta = 1.945$, $\Delta = 2.048$ with an average for the four of $\bar{\Delta} = 1.950$. There can, therefore, be no legitimate assumption that the constant for the host is too high. There seems, indeed, no valid objection to this exception to the rule of a higher osmotic pressure of the juices of the parasite.

In its bearing upon the problem of the relative osmotic pressure of the solutions in the tissues of the two organisms the following cases of two or more species of parasites occurring on the same host plant are of great interest.[14]

The cases are arranged by the hosts.

204.	*Baccharis scoparia*	$\Delta = 1.15$,	$P = 13.8$
	Phthirusa parvifolia	$\Delta = 1.42$,	$P = 17.1$
	Dendrophthora cupressoides	$\Delta = 1.19$,	$P = 14.4$
247.	*Baccharis scoparia*	$\Delta = 1.28$,	$P = 15.4$
	Phthirusa parvifolia	$\Delta = 1.50$,	$P = 18.0$
	Dendrophthora cupressoides	$\Delta = 1.26$,	$P = 15.1$
265.	*Dodonea jamaicensis*	$\Delta = 1.41$,	$P = 16.9$
	Phthirusa parvifolia	$\Delta = 1.63$,	$P = 19.6$
	Phthirusa paucifolia	$\Delta = 1.71$,	$P = 20.5$
	Phthirusa lepidobotrys	$\Delta = 1.59$,	$P = 19.1$
292.	*Durantia repens*	$\Delta = 1.29$,	$P = 15.5$
	Phthirusa parvifolia	$\Delta = 1.40$,	$P = 16.8$
	Phthirusa lepidobotrys	$\Delta = 1.39$,	$P = 16.7$

---

[13] This is also true of *D. cupressoides* on Baccharis discussed in a preceding paragraph.

[14] In collecting samples of this kind it was often impossible to secure ample materials of both of the parasites from the same shrub or tree. In such cases great care was taken to obtain materials of both parasites from the same individual trees and to compound the sample of the host plant from these trees in order to avoid all possibility of having the comparability of the samples jeopardized.

481. *Palicouria alpina* .... $\Delta = 0.83$, $P = 10.0$
    Phthirusa parvifolia .... $\Delta = 1.23$, $P = 14.8$
    Dendrophthora gracilis .... $\Delta = 1.12$, $P = 13.5$
484. *Vaccinium meridionale* .... $\Delta = 1.32$, $P = 15.9$
    Phthirusa parvifolia .... $\Delta = 1.39$, $P = 16.7$
    Dendrophthora gracilis .... $\Delta = 1.34$, $P = 19.1$

In all, the osmotic pressure of the juices of each of the two or three parasites is higher than that of the host, although they may differ sensibly between themselves.

One of the most interesting cases is that of a broad-leaved loranth, *Phthirusa parvifolia* parasitic upon a leafless member of the same family, *Dendrophthora gracilis* which is in turn parasitic upon a tree of *Cyrilla racemiflora* about twenty feet in height (Coll. 196).

The sap properties stand in the following relationship.

Cyrilla racemiflora .... $\Delta = 1.18$, $P = 14.2$
Dendrophthora gracilis .... $\Delta = 1.26$, $P = 15.2$
  (on *Cyrilla racemiflora*)
Phthirusa parvifolia .... $\Delta = 1.49$, $P = 17.9$
  (on *Dendrophthora gracilis*)

Osmotic pressure increases from host to the primary parasite and from the primary parasite to the secondary one.

Note also that the observed secondary parasitism is *Phthirusa parvifolia* with an average depression of 1.35° upon *Dendrophthora gracilis* with an average depression of 1.18°.

Whether the reciprocal case of secondary parasitization ever occurs could only be determined by more extensive field observation.

IV. Discussion of Results

The demonstration of the lower osmotic pressure of the tissue fluids of the leafless as compared with the leafy species of Loranthaceae requires no special discussion at the present time. The validity of this conclusion, based primarily upon averages, although also evident in the general trend of the individual constants, is evidenced for by certain favorable combinations of parasitism.

In four cases (Col. 204, 247, 481, 484) it was possible to secure determinations from a leafless and a leafy form upon the same host. As shown by the table above, the osmotic pressure of the leaves is higher in each case than that of the stems of the associated leafless parasite.

Note also that in the instance of secondary parasitism noted above, the primary parasite is leafless (Dendrophthora) and the secondary parasite (Phthirusa) leafy.

The problem of the relative magnitudes of the osmotic pressures of the fluids of parasites and host merits a short theoretical discussion.

Let P_h be the observed pressure of the solution h in the tissues of the host, and P_p the observed pressure of the solution p in the tissue of the parasite. Then at first thought

$$P_p > P_h$$

would seem to be the necessary condition for the absorption of water from the host by the parasite. It is as a matter of fact the relationship almost always, but apparently not invariably, found. The view that it is the essential condition is of course quite fallacious, since p is not drawing water directly from h but the two are obtaining their water and its solutes from a common source, say t, the solution in the tracheae, with osmotic pressure P_t, which must be assumed to be less than that of either the solutions in the leaves of the host or the tissues of the parasites.

Now nothing is known concerning the concentration of the solutions in the xylem of the species upon which our determinations were based, but *a priori*, there should be no question in the minds of botanists that the osmotic pressure of the sap surrounding the haustoria of the parasite is distinctly lower than that of the leaf cells. Those who desire authority in support of this view may turn to the classic statement of Sachs that the water in the tracheae is an exceedingly dilute solution of nutritive salts which may be compared at once to ordinary drinking water.

Fortunately direct evidences are available for trees of temperate regions. Dixon and Atkins (1914, 1915) have given the following values for sap centrifuged from the wood in comparison with those obtained from the leaves after treatment with liquid air.

For *Acer pseudoplatanus*, in August
  from tracheae of root . . . . $\Delta = 0.070$
  from tracheae of branch . . . . $\Delta = 0.049$
  from tissue of leaf . . . . $\Delta = 1.207$
For *Populus alba*, in August
  from tracheae of root . . . . $\Delta = 0.072$
  from tracheae of stem . . . . $\Delta = 0.047$
  from tissue of leaf . . . . $\Delta = 1.487$

Clearly the values found for the leaves are enormously greater than those for the sap from the non-living conducting tissue of the stem. Further determinations for the wood of stem and root in *Acer pseudoplatanus*, *Cotoneaster frigida*, *Fagus silvatica*, *Ilex aquifolium*, *Populus alba* and *Salix babylonica* indicate that while the concentration of the fluids centrifuged from these stems varies rather widely during the year, concentrations comparable to those of the foliage leaf are never found. Indeed, the observed depression of such fluids is only a fraction of that prevailing in the leaf tissue of the typical arborescent plant.

Thus if the trunks of the ligneous hosts from which our parasites were taken present no higher concentrations in their fluids than do those of the trees studied by Dixon and Atkins,[15] there would seem to be no reasonable question of the adequacy of the osmotic pressures demonstrated in both the leaves of the host and the tissues of the parasite for any rôle which may be logically assigned it in maintaining a flow of water from the wood cells to the chlorophyll bearing tissues of both host and parasite.

Thus the condition

$$P_h > P_t, \quad P_p > P_t$$

where h represents the leaves and t the conducting system of the trunk of the host, may be reasonably assumed to obtain universally in the case of shrubby parasites on the aerial parts of the ligneous hosts.

Returning to the question of the relative values of P_h and P_p it is now evident that these merely draw from t in competition with each other. Were the supply of t inadequate then $P_p > P_h$ would be a necessary condition for the development of the parasite, but if the supply of t is not limited it seems theoretically quite possible for a parasite to flourish on a host which has leaves of a higher osmotic pressure drawing water from the vascular system in competition with it.

In such competition h would draw water from t until the osmotic pressure of the cell came into equilibrium with the tension of the surrounding cell wall. The rate of absorption would then be limited by this tension, and *p* would be free from the competition of *h* so long as the volume of *t* was sufficient for both. In just such a region as the Blue Mountains of Jamaica, with its heavy and well distributed precipitation, one would expect the water brought up from the soil to be continually adequate.

---

[15] Incidentally it may be pointed out that if the conclusion reached by Dixon and Atkins, that sugars (monosaccharides, disaccharides or both) are found at all times in the tracheae of trees, be found to apply generally to ligneous plants, new light is thrown upon the much discussed question of the degree of parasitism in the Loranthaceae. Even if they draw their substance entirely from the xylem they can hardly be regarded as merely water and mineral parasites, provided the tracheae contain throughout the year sugars supplied from the cortex by way of the medullary rays and the wood parenchyma, as urged by Dixon and Atkins. The discussion of this point falls quite outside the scope of the present paper.

There now seems ample comparative evidence for the soundness of the reasoning here involved. Dixon and Atkins in a series of studies (1912, 1912*a*, 1912*b*, 1915*a*) have shown by very exact work on *Ilex aquifolium*, *Hedera Helix* and *Syringa vulgaris* that the osmotic pressure of the young leaves is generally lower than that of the older ones. We have in our own unpublished data constants for a wide range of species from rain forest, desert and mesophytic habitats. These show that in general lower osmotic pressure characterizes the sap of the young leaves. Nevertheless it is quite obvious that these young leaves are drawing water in competition with the old ones.

It is important to note that in the cases in which determinations were based upon the tissue fluids of young leaves as well as upon those of the old leaves of the host, the osmotic pressure of the juices of the parasite has always been found to be higher than that of the young leaves.

Most convincing evidence of the same kind is furnished by our studies of prolification of the fruit in Passiflora (Harris, Gortner and Lawrence, 1915). In this remarkable abnormality a whorl of incompletely fused carpels is formed inside the trimerous or tetramerous ovary wall. Extensive observations have shown that for electrolytes, measured by electrical conductivity, and for both electrolytes and non-electrolytes, measured by specific gravity and by freezing point lowering, the concentration of the fluids of the abnormal structure is almost invariably lower than that of the normal wall, in competition with which it must draw its solutions from the conducting system of the plant.

V. Recapitulation

In this paper, which is one of a series on various physiological, ecological and phytogeographical problems involving the investigation of the physico-chemical properties of vegetable saps, we present data on the osmotic pressure of the tissue fluids of tropical mistletoes parasitic on various ligneous hosts.

Osmotic pressure has in every case been calculated from the depression of the freezing point of saps extracted by pressure from previously frozen tissues. The conclusions are based upon 42 pairs of determinations distributed among seven species belonging to three genera of Loranthaceae parasitic on 19 species of host. All determinations here published were made on materials collected in the neighborhood of Cinchona, in the Blue Mountains of Jamaica.

These studies demonstrate with reasonable certainty:

(*a*) That the sap extracted from the tissue of the green stems of the leafless species belonging to the genus Dendrophthora are characterized by a lower osmotic pressure than that obtained from the leaf tissue of the leafy species of Phoradendron and Phthirusa. These are of the order 1.170° and 1.350° freezing point lowering or about 14.2 and 16.2 atmospheres pressure respectively.

(*b*) That the osmotic pressure of the sap extracted from the chlorophyll bearing tissues of the parasite is almost always, but apparently not invariably, greater than that expressed from the mature leaves of the host.

While higher osmotic pressure of the sap of the parasite is a general condition, we have shown that it is not a *necessary* condition for at least the temporary success of the parasite. The parasite should be able to draw from the relatively dilute solutions in the stem in competition with organs of actually higher osmotic pressure, except at periods when the supply of soil moisture is limited, just as young leaves are able to draw water in competition with old leaves of higher osmotic pressure.

In conclusion we have to express our hearty thanks to Professor Bower and the other members of the British Association Committee having in charge the Tropical Laboratory at Cinchona for its protracted use, to Dr. MacDougal, director of the Department of Botanical Research, for material assistance in field operations, and to Dr. Britton, for the opportunity of having the materials upon which this and other unpublished physiological studies on Jamaican plants were based critically examined at the Herbarium of the New York Botanical Garden. To Mr. Percy Wilson of the Garden we are indebted for the painstaking care with which this work was carried out. To Mr. Wm. Harris, F.L.S., Superintendent of Public Gardens and Plantations, Jamaica, we are indebted for many courtesies which contributed

not merely to the success of our work but to the pleasure of our stay in Jamaica.

Station for Experimental Evolution,
Cold Spring Harbor, N. Y.

LITERATURE CITED

Dixon, H. H. Transpiration and the Ascent of Sap in Plants. Macmillan & Co. 1914.

Dixon, H. H. and W. R. G. Atkins. Changes in the Osmotic Pressure of the Sap of the Developing leaves of *Syringa vulgaris*. Sci. Proc. Roy. Dublin Soc. n. ser. **13**: 219–222. 1912.

Dixon, H. H. and W. R. G. Atkins. Variation in the Osmotic Pressure of the Sap of *Ilex aquifolium*. Sci. Proc. Roy. Dublin Soc. n. ser. **13**: 229–238. 1912.

Dixon, H. H. and W. R. G. Atkins. Variations in the Osmotic Pressure of the Sap of the Leaves of *Hedera Helix*. Sci. Proc. Roy. Dublin Soc. n. ser. **13**: 239–246. 1912.

Dixon, H. H. and W. R. G. Atkins. Osmotic Pressures in Plants, IV. On the Constituents and Concentration of the Sap in the Conducting Tracts, and on the Circulation of Carbohydrates in Plants. Sci. Proc. Roy. Dublin Soc. n. ser. **14**: 374–392. 1915.

Dixon, H. H. and W. R. G. Atkins. Seasonal Variations in the Concentration of the Cell Sap of Some Deciduous and Evergreen Trees. Sci. Proc. Roy. Dublin Soc. n. ser. **14**: 445–461. 1915.

Gorke, H. Über chemische Vorgänge beim Erfrieren der Pflanzen. Landwirthsch. Versuchs. Stat. **65**: 149–160. 1906.

Harris, J. Arthur and R. A. Gortner. Note on the Calculation on the Osmotic Pressure of Expressed Vegetable Saps from the Depression of the Freezing Point, with a Table for the Values of P for $\Delta = .001°$ to $\Delta = 2.999°$. Amer. Journ. Bot. **1**: 75–78. 1914.

Harris, J. Arthur, R. A. Gortner and J. V. Lawrence. A Comparison of the Physico-Chemical Constants of the Juices Expressed from the wall and from the Included Carpellary whorl in Proliferous Fruits of *Passiflora gracilis*. Biochem. Bull. **4**: 52–79. 1915.

MacDougal, D. T. An Attempted Analysis of Parasitism. Bot. Gaz. **52**: 249–260. 1911.

MacDougal, D. T. Induced and Occasional Parasitism. Bull. Torrey Club **38**: 473–480. 1911.

MacDougal, D. T. and W. A. Cannon. The Conditions of Parasitism in Plants. Publ. Carn. Inst. Washington **129**. 1910.

Shreve, F. A Montane Rain Forest. A Contribution to the Physiological Plant Geography of Jamaica. Publ. Carn. Inst. Washington **199**. 1914.

York, H. H. The Origin and Development of the Embryo Sac and Embryo of *Dendrophthora opuntioides* and *D. gracilis*. Bot. Gaz. **56**: 89–111, 200–216. 1913.